Cognition in contests: mechanisms, ecology and evolution

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ABSTRACT

Animal contests govern access to key resources and are a fundamental determinant of fitness within populations. Little is known about the mechanisms generating individual variation in strategic contest behavior or what this variation means for population level processes. Cognition governs the expression of behaviors during contests, most notably by linking experience gained with decision making, but its role in driving the evolutionary ecological dynamics of contests is only beginning to emerge. We review the kinds of cognitive mechanisms that underlie contest behavior, emphasize the importance of feedback loops and socio-ecological context, and suggest that contest behavior provides an ideal focus for integrative studies of phenotypic variation.

A role for cognition in competition

Competition for resources such as food, mates and territories is ubiquitous among animals and a fundamental predictor of fitness [1]. Much of this competition is mediated by contests (see Glossary), in which animals use specialized aggressive displays and overt physical attacks to determine access to resources [2]. Contests are incredibly variable both within and between species in their format, intensity and the specific behaviors involved [2]. Understanding the causes and consequences of animal contest behavior is important because aggressive interactions affect social structure and individual fitness, which can carry over to impact key higher-level processes including selection, population dynamics and distribution [3–5]. Contests require rapid information processing for decision making about when, how and with whom to challenge, escalate or withdraw [6]. We argue that cognition provides a significant but largely unexplored explanation for variation in contest behavior because cognitive mechanisms such as learning from previous interactions, and assessments of resource value, physical ability and social status, facilitate information processing and decision making.

Examining cognitive mechanisms will provide important new insights for studies of animal contests. First, although evidence abounds for a role of cognition in contests (Table 1), most studies focus only on demonstrating that animals gather and use information. The mechanisms by which this information is processed, retained and employed in decision making are rarely investigated and largely treated as a black box by both empiricists and theoreticians [7]. However, these mechanisms are critical to understanding variation between individuals and between species in contest behavior because cognitive processing might not always lead to optimal behavioral expression, as is commonly assumed [8]. Constraints on

information gathering and use might explain why contest assessments often incorporate only a limited subset of the available information [9], and why individuals with lower resource-holding potential (RHP) sometimes can bluff their way to success by deceiving their opponents [10]. Second, focusing on cognition emphasizes that animal contests are not one-time, context-independent events, but rather take place within a series of interactions across individuals' lifetimes in a complex environmental and social milieu. Cognition links experience gained in past interactions to future contest behaviors. Third, RHP, the key variable determining contest success [11], is often estimated using a single physical characteristic (i.e., body size) but is in fact a composite trait with inputs from multiple phenotypic characteristics [12]. We argue that cognitive performance is often an important component of RHP, and can sometimes reduce or even override advantages accruing to larger individuals.

In an effort to understand the diversity of animal contest behavior, we present evidence that cognition underlies important behaviors involved in animal contests (Table 1). We examine these behaviors within a general framework for testing hypotheses about how links between cognition and contest behavior influence evolutionary and ecological processes, with the potential to feed back onto cognitive and behavioral traits (Figure 1). We discuss how these feedback mechanisms could explain the causes and consequences of both individual, within-species, variation in cognitive performance, and between-differences in the role of cognition in contests. Recently, major advances have been made in developing cognitive assays for field and laboratory studies [13], methods to elucidate the neural bases of cognition [14] (**BOX 1**), statistical analyses of contests [15], measurements of selection on cognitive traits [16] and monitoring individuals within ecologically relevant contexts in complex social

environments [17]. Our aim is to encourage researchers to apply these tools and methodologies towards integrative studies of cognition and contest behavior.

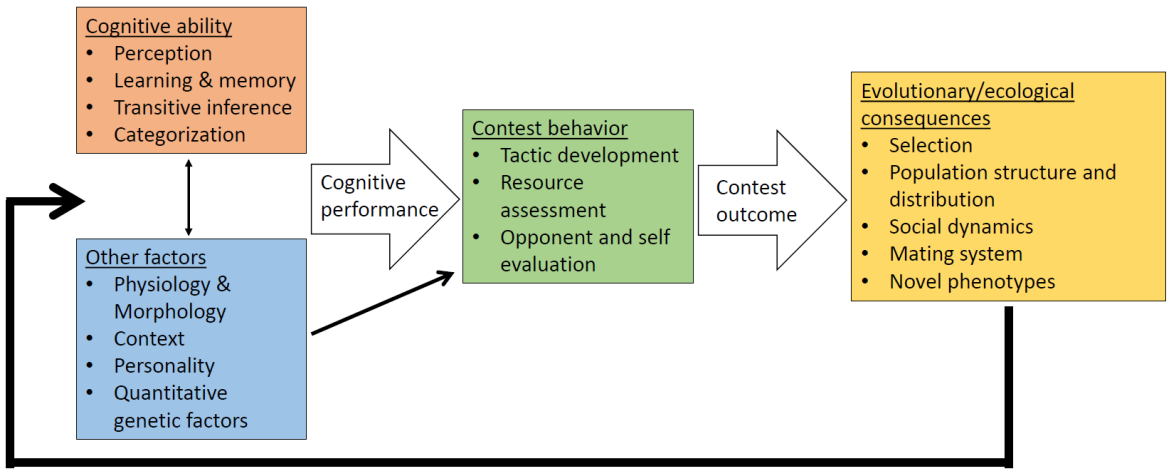

Figure 1. A framework for the integrative study of cognition and animal contests. Cognitive performance is determined by the interaction between cognitive abilities and other factors, including both internal (e.g., physiological state) and external (e.g., environmental context) factors. Variation in cognitive performance affects the expression of contest behaviors, to the extent that these behaviors involve cognition. Other factors can directly affect contest behavior, and also indirectly affect contest behavior through effects on cognitive factors. Variation in contest behavior, including that resulting from variation in cognitive performance, influences the dynamics and outcome of contests, determining the costs and benefits for contest winners and losers. The magnitude of these costs and benefits determines the evolutionary and ecological consequences of variation in contest behavior, including variation in fitness as well as the distribution of individuals in space and with respect to social group members. These effects on fitness, social structure and ecology then lead to feedback mechanisms on the aggressive behaviors, and on the associated cognitive and non-cognitive mechanisms.

Cognitive mechanisms of contest behavior

Cognition encompasses a diverse range of mechanisms for information acquisition, processing and use, including perception, learning and memory, individual recognition and transitive inference of social status [18]. Identifying the specific cognitive mechanisms of contest behaviors is an important but challenging task. For instance, opponent recognition is often important in contests and can arise from habituation learning [19], categorization of different classes of individuals [20], or so-called 'true' individual recognition [21]. Furthermore, it is difficult to disentangle the effects of cognition, personality, motivation and condition on behavioral expression, and the careful experimental designs required to distinguish between these factors are challenging even for the most tractable species [22]. Nevertheless, cognitive mechanisms are known or hypothesized to be important in many species' contests; we discuss the evidence here, which provides a solid basis for further study of contests and cognition (**BOX 2**).

Development of signals and tactics

The skill with which individuals perform aggressive displays and fighting maneuvers has recently been identified as a significant, but understudied, determinant of contest success [23]. Learning likely facilitates the development of skills important in contests. Bird song is used in territorial contests and many song characteristics are learned during juvenile development [24], raising the possibility that learning enables birds to produce more effective aggressive signals. In song sparrows *Melospiza melodia*, young birds learned more songs from tutors that they had competed with aggressively [25]. Most studies of song learning

115 focus on song structure and syntax, and less is known about learning of song performance
116 (e.g., timing, amplitude, type matching) [26], which is especially important in bird contests
117 [27]. Animals can also learn improved fighting tactics from recent contest experiences. For
118 instance, three-spined sticklebacks *Gasterosteus aculeatus* learned the association between
119 producing threat displays and causing an opponent to flee, likely through operant
120 conditioning [28]. Blue gouramis *Trichogaster trichopterus* and *Betta splendens* learned via
121 classical conditioning to anticipate, respectively, the timing and direction of a rival's
122 approach [29,30]. Learning might even enable animals to adjust their tactics during contests
123 by monitoring the effectiveness of contest behaviors. In fights over shell ownership in hermit
124 crabs *Pagarus bernhardus*, individuals prevented from effectively rapping opponents' shells
125 shifted to an alternative tactic of rocking opponents' shells [31]. Cognition is likely involved
126 in such tactical adjustments, but the cognitive mechanisms have not been investigated to date.
127
128 *Assessment strategies*
129
130 Once a contest has begun, contestants must rapidly decide how to behave and whether to
131 persist, withdraw or escalate. These decisions are determined by the individual's assessment
132 strategy [11]. Different models of strategic contest behavior propose assessment strategies
133 differing primarily in how individuals use different sources of information to determine their
134 behavior [32]. Individuals can assess their own state, their opponent's characteristics, the
135 value of the disputed resource and the social context in which the contest takes place [6,33].
136 The extent to which cognitive processes underlie different assessment strategies has received
137 surprisingly little study and remains controversial (**Box 3**).
138

Assessments of resource value might be especially amenable for cognitive studies because both the resource itself and contestants' experience with the resource are relatively easily manipulated. Asymmetries in information about resources often determine individual persistence in contests [6], although most studies manipulate opportunities to access information (e.g., by only pre-exposing one of the two contestants to the resource; [34]) rather than examining variation in cognitive abilities such as memory for specific information about resource quality. In the context of our framework, it is important to study why individuals or species vary in their ability to gather, process and retain information on resource value, and how these cognitive mechanisms interact with other decision making processes during contests [35]. Indeed, studies of resource-value assessment have shed light on cognitive processes such as attention. For instance, resource value only affects contest persistence in round gobies *Neogobius melanostomus* when individuals had previous experience with the resource, and individuals were limited in the ability to readjust resource valuation during contests, possibly because of constraints on attention [36].

Opponent evaluation

Studies of assessment strategies often focus on information gathering and decision making during contests. However, information gathering about opponents also takes place before and after contests, and the ability to learn from these experiences is likely a major determinant of an individual's subsequent contest behavior, including decisions to instigate further contests. Sometimes perceiving an opponent's physical characteristics suffices to identify a superior rival [33]. However, many other cognitive mechanisms allow individuals to make more accurate or detailed assessments of their opponents.

Individuals might learn about opponents indirectly by social eavesdropping. By observing contests, individuals obtain information about the relative abilities of the contestants and use this to determine their response to those contestants in the future [37]. Social eavesdropping requires learning and memory of both the identity and fighting ability of the observed contestants. The cognitive mechanisms underpinning social eavesdropping were investigated in barn owls *Tyto alba*. Juveniles eavesdrop on competitive vocal interactions between siblings, and memory retention depended on the frequency of exposure to sibling vocalizations [38]. This suggests that limitations on receiver memory impose selection pressures on signalers to repeat displays, which could partly explain the commonly-observed but theoretically puzzling phenomenon of animal displays composed of rapid repetitions of the same signal [39].

Individuals can also learn about opponents from direct previous experiences. Opponent recognition might involve categorization of opponents into classes. For instance, snapping shrimp *Alpheus heterochaelis* that had previously lost contests recognize and escape rapidly from previous contest winners, regardless of whether they had experience with that particular opponent, suggesting categorization based on a general phenotype rather than individual recognition [40]. Other species might be capable of true individual recognition [21]. In Iberian wall lizards *Podarcis hispanica*, males recognize the scent marks of several individual rivals and remember where rivals left scent marks in relation to their own territory, using this discrimination ability to modulate their behavior accordingly in future contests based on the relative threat of recognized individuals [41]. True individual recognition could be invoked because subjects associated individual-specific opponent characteristics (scent mark composition) with individual-specific information about opponents (spatial scent marking behavior) [21]. Opponent recognition is particularly important in territorial species;

individuals often show ‘dear enemy’ relationships with territorial neighbors, responding less aggressively to these individuals than to unrecognized strangers [42]. In bullfrogs *Rana catesbaeiana*, the dear enemy effect is mediated by habituation learning of both acoustic signal characteristics and spatial locations of individual neighbors [43]. Direct and indirect information might be integrated to inform decisions. Eavesdroppers could use transitive inference, allowing them to determine not only the relative qualities of the observed competitors with respect to each other, but also with respect to the eavesdropper’s own competitive status [44].

Own status evaluation

Learning about self might be an important component of winner and loser effects, in which winners of previous contests tend to continue winning, and losers tend to continue losing [45]. The cognitive mechanisms involved have not been investigated explicitly, but in male *Anolis carolinensis* lizards, the effects of changes in physiological state on loser effects were at least partly ruled out, suggesting that loser effects formed because of changes in how individuals perceived their own fighting ability [46]. Stronger evidence for a role of cognition on winner and loser effects comes from species in which these effects are only shown, or are stronger, against familiar individuals, implying an important role of learning and memory. Hermit crabs *Pagurus middendorffii* that lost a fight recognize previous opponents and avoid combat with them, while showing no behavioral changes in response to unfamiliar individuals [47]. The explicit role of memory in winner and loser effects was investigated in *Drosophila melanogaster*, where memory of previous winning or losing experiences decays more slowly in contests involving familiar individuals [48]. If winner and loser effects arise from individuals learning more about their own fighting abilities, then memory will interact

214 with assessment in future contests. Namely, more experienced individuals should more
215 rapidly assess their quality relative to an opponent; thus, winner and loser effects should
216 affect not only the outcome, but also the duration and escalation of future contests.
217
218 **Cognitive performance and individual variation**
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220 Consistent between-individual variation in contest behavior and success has been
221 demonstrated in many species [49]. Most empirical studies examine the morphological and
222 physiological components of RHP to explain this variation [33]. We have argued that
223 cognition is an important component of many contest behaviors; thus, variation in cognitive
224 performance could be a major source of individual variation in RHP. However, evidence for
225 links between cognitive performance and individual RHP is scarce. Cognitive performance in
226 contests might vary because individuals vary in cognitive ability. For instance, if contest
227 behaviors are learned, some individuals could learn more rapidly than others, giving them an
228 advantage. The conditioning protocols described above for learning to anticipate rival
229 approach could be utilized to determine if those individuals that learned the task more readily
230 were especially likely to win contests and resolve them quickly. Similar approaches could be
231 utilized for neighbor recognition learning: do individuals that learn to recognize new
232 neighbors more rapidly in playback experiments instigate fewer aggressive interactions with
233 their actual neighbors?
234
235 Individuals might also vary in the extent to which they strategically utilize cognitive abilities
236 in contests [9,50]. This could be tested by measuring how sensitive individuals are to
237 variation in opponent signal characteristics. Some individuals might carefully assess
238 opponent signals and even recognize specific opponents and adjust their response

accordingly, whereas others respond similarly to all opponents [9]. The latter individuals are predicted to have superior physical characteristics if there are trade-offs between cognitive and non-cognitive competitive abilities [51], suggesting the possibility of alternative stable strategies [52]. Finally, cognitive performance is likely to be context dependent. Different ecological and social conditions create greater or lesser challenges for cognitive performance in contests, and individuals differ in their previous experiences. Manipulations of individual experiences are straightforward, and have been employed often in studies of age effects on contest dynamics [53], and winner and loser effects [54].

Evolution, ecology, cognition and contests

Cognition is both a driver of variation in competitive ability leading to variation in fitness-related resource acquisition, and is itself likely to be affected by selection acting on contest behavior (Figure 1). Contest behavior is intimately related to the distribution of individuals and resources in the environment, which determines contest frequency, the benefits of success, and the quality of information for cognitive processing. Ecology is therefore likely to be a key consideration in explaining why species differ in the role of cognitive mechanisms in contests. Below, we outline several hypotheses that relate cognition, contest behavior and ecological or evolutionary processes.

Cognitive performance and fitness

Identifying the fitness consequences of individual variation in cognitive performance is a major focus of recent studies in wild populations [55]. While cognitive performance can impact individual fitness via contest success (Figure 1), little is known about how frequent or

strong these impacts are in natural populations. It is also unknown the extent to which benefits of higher cognitive performance in contests are counteracted by costs, and what the net impact is on fitness [56]. Indeed, few studies have quantified fitness benefits or investigated whether these gains balance the costs of resource acquisition and defense for any contest behavior [57]. Specific fitness costs of cognitive performance in contests might be linked to energetic costs of neural tissue development and maintenance, which trade off with investment into non-cognitive components of RHP, and with cognitive abilities in other contexts [51]. Likewise, fitness costs of poor competitiveness might be counteracted by superior cognitive performance in other contexts. Great tits *Parus major* that were less successful in contests over food had greater innovative tendencies and survived equally well as more successful competitors, potentially because they could exploit novel food resources [56].

For there to be a response to any selection acting on cognitive performance in contests, cognitive performance must be heritable. However, little is known about the heritability of any cognitive trait in wild populations [58], or of the repeatability of cognitive performance over time, and relationships between competitive ability and cognition can also arise from plasticity rather than heritable variation [59]. Demonstrating such a response to selection is difficult, but measurements of selection on cognitive traits and their heritability have been made in other contexts [16,58] and similar approaches could be applied to study cognition and contests. Additional theoretical studies incorporating cognitive mechanisms (**Box 4**) would also improve the understanding of the population-level consequences of cognition and contests.

Social structure and contest cognition

289

290 Social group size and stability affects the opportunities for learning about opponents, and also
291 the value of such information. Between-species variation in whether contests are resolved
292 primarily by individual recognition learning or by signal exchanges (badge of status
293 recognition, which does not necessarily require learning) is hypothesized to be related to
294 variation in opportunities for learning about opponents in social groups [60]. In species with
295 small, stable social groups and repeated interactions, there are many opportunities to learn
296 each group member's capabilities, and individual recognition should determine when contests
297 are instigated and how they are resolved. In contrast, when social groups are large and/or
298 unstable, there is less opportunity for learning and individuals are predicted to use badges of
299 status for opponent assessment [60]. This hypothesis could also explain within-species
300 variation. For instance, male *A. carolinensis* assess visual signals (darkened eyespots, a badge
301 of status) of unfamiliar opponents, but in subsequent fights with a familiar opponent they
302 behaved according to its previous dominance even if the opponent's visual signals were
303 manipulated, indicating the opposite rank [61]. More generally, the costs and benefits of
304 strategies incorporating cognition or other assessment mechanisms will determine which
305 strategy predominates in a given situation. Elephant seals *Mirounga angustirostris* provide an
306 intriguing example: despite the social group's large size and fluidity, recognition learning of
307 individual acoustic signatures is important for rival assessment because costs of fighting are
308 particularly extreme in this species [62].

309

310 The 'Machiavellian intelligence' hypothesis argues that individuals in stable social groups are
311 selected to attend to other group members' interactions, especially dominant and subordinate
312 relationships determined by contests (e.g., via social eavesdropping, see above).
313 Machiavellian intelligence might have been important in the evolution of social cognition

among primates [63], and could explain hominid brain evolution [64]. Attention to the perspectives and knowledge held by other group members is an important component of theory of mind [65]. Although the notion that animals have anything approaching human-like capabilities in this regard is highly controversial [66], this could conceivably operate to some degree in some species and allow for novel contest strategies. For instance, subordinate chimpanzees are sensitive to whether a specific dominant individual had observed the location of hidden food, and preferentially forage in places where the dominant had not observed food being placed, thus avoiding contests [67]. Understanding others' intentions also raises the possibility of tactical deception in animal contests. In three monkey species, subordinate individuals withheld information from dominants about the location of food; interestingly the efficiency of deception was inversely related to the strictness of the dominance hierarchy and social group stability, indicating feedbacks between contests and cognitive abilities [68]. Furthermore, group living might have selected for the evolution of numerical competence because individuals assess numerical asymmetries in group size during intergroup contests [69].

Diet, stress, dominance and cognition

Because many animal contests are disputes over food, contest success might impact individual ability to obtain resources necessary for developing and maintaining cognitive capabilities. The developmental stress hypothesis argues that birdsong is a good indicator of male quality for female mate choice because song is learned during a critical developmental period when individuals are likely subject to multiple stressors; birds producing quality song were less stressed during development [70]. Success in resource acquisition should reduce developmental stress, and is in part mediated by contest competition, generating feedbacks

between contests, stress and cognition. Although the developmental stress hypothesis is usually applied to birdsong, it should apply to the development of any cognitive trait, including those involved in contests during adulthood [71]. Thus, contest success during development can have cascading effects on the cognitive abilities required for future contest success, potentially driving individual differences in competitive ability.

Stress during adulthood affects both cognition and contest success in species with dominance hierarchies, but these effects depend on how hierarchies are maintained. Dominant individuals are the most physiologically stressed in species in which dominance is maintained by frequent overt aggressive acts towards subordinates, while lower-ranking individuals tend to be more stressed in species in which dominance is maintained primarily by signaling [72]. Such chronic stress often impacts on cognition [73].

Concluding Remarks

Cognition plays an important role in all stages of contests across a wide taxonomic range. That the cognitive mechanisms of contest behavior and the ecological and evolutionary implications of cognitive variation in contests remain largely unknown, even when intriguing hypotheses exist, reflects the focus of cognitive ecologists and psychologists on other animal behaviors, and the focus of behavioral ecologists on ultimate causation in contest studies. The time is ripe to study cognitive mechanisms in animal contests (**Outstanding questions box**) because contests exemplify many of the major themes in contemporary cognition and behavioral ecology research: there is substantial variation in contest behaviors, with repeated interactions in complex social environments and involving information gathering abilities that might trade-off with such abilities in other contexts. Our framework synthesizes the diverse

364 knowledge of cognitive processes in contests and provides an appropriate context for studies
365 integrating evolutionary consequences of variation in strategic contest behavior and the
366 mechanisms generating variation in cognitive performance in wild animals.
367

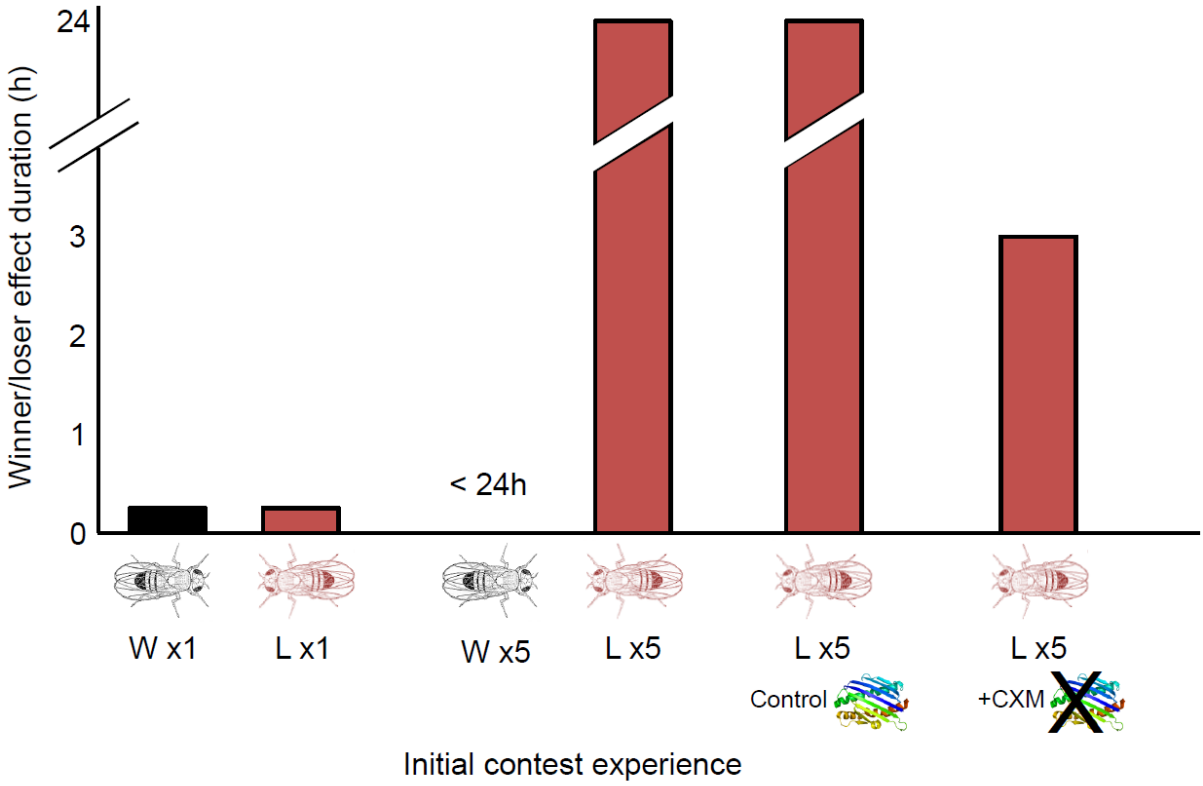
Box 1 – Neural mechanisms, cognition and contest behavior

Identifying the neural processes underlying cognitive mechanisms of animal contest behavior provides insight into the origins of differences between individuals and species in cognitive abilities. Below we summarize some of the few studies explicitly linking activity in the brain to cognitive traits expressed in contests.

Drosophila melanogaster show loser effects, and these are stronger when losers are paired against familiar individuals, suggesting a role of memory in contests [74]. Indeed, both short- and long-term memory are involved in the formation of loser effects, with the duration of the memory depending on the number of repeat losses [48]. Short- and long-term memories have different neural substrates (Figure I). Long-term memories of losing experiences arise via protein synthesis occurring during or after contests; when protein synthesis is blocked, the short-term loser effect remains but long-term loser effects disappear [48]. However, specific genes that affect memory formation in *D. melanogaster* contests have not been identified. Hearing has been identified as a critical sensory mechanism regulating aggression in *D. melanogaster*. Inhibiting neurotransmitter release in specific peripheral auditory neurons strongly reduced aggression levels [75].

In *Anolis carolinensis*, individuals recognize previous opponents and form dear enemy relationships with territorial neighbors [76]. The neuroendocrine response of individuals to an aggressive challenge depends on its status (dominant or subordinate) and on the opponent's familiarity [77]. Dominant males exposed to familiar opponents had higher epinephrine levels

in the hippocampus, and in general social interactions led to increased activity of NMDA receptor subunits in the hippocampus [78]. Because the hippocampus is involved in spatial and social learning [79], these neuroendocrine responses might be involved in the formation of memories related to dear enemy behavior.



Box 1, Figure I. Mechanisms of long-term memory formation in *D. melanogaster* contests. Winner and loser flies from an initial contest trial were assayed for winner and loser effects by testing whether they were more likely to win or lose, respectively, a contest against a naïve individual. Bars show the duration of winner (black) or loser (red) effects. Winner and loser effects disappeared rapidly after a single contest experience. However, losers, but not winners, of five consecutive contests against the same opponent had altered contest behavior and success 24 hours later. Flies treated with cycloheximide, which inhibits protein synthesis, showed a short-term but not a long-term loser effect, demonstrating that *de novo* protein synthesis is the mechanism responsible for this long-term memory formation. After [48].

Box 2 – Experimental approaches for studying cognition and contests

Although cognition clearly plays a role in many animal contest behaviors, the specific cognitive mechanisms are not always identified, and the relative importance of cognitive and other factors is rarely quantified. Here we outline some potentially fruitful experimental approaches to identify the cognitive mechanisms of contest behavior and determine the sources of individual variation in cognitive performance.

1. Independently manipulating the quality of information available to each contestant for assessment and learning, for instance by interfering with sensory perception, the duration and nature of previous experience, and opponent appearance. Playbacks could be used to mismatch signal characteristics with actual opponent quality; if the relationship between opponent signals and quality is learned, then individuals trained in the mismatched treatment should respond inappropriately in natural contests. Experimental manipulations of the proximate underpinnings of cognition, such as neural processing (**Box 1**), stress levels at critical developmental periods, or gene expression, are especially powerful techniques.

2. Training individuals to perform the hypothesized cognitive task in another context and then assaying their contest performance. For instance, mutual opponent assessment involves the evaluation of opponent quality relative to self quality [80]. Individuals trained to perform well in relative assessments in other contexts, such as choosing between two different amounts of food, might therefore be expected to be better at mutual assessment in contests (i.e., to resolve contests more quickly and accurately). The utility of this approach depends on the extent to which performance of a cognitive task in one context carries over to other

contexts [13]. Furthermore, if cognitive load limits learning and memory [81], individuals that recently learned a relatively complex task might be less able to perform cognitively demanding assessment during contests than individuals with no, or less challenging, previous learning experience.

3. Assays of generalization in opponent recognition. If individuals recognize categories of opponents, then manipulation of opponent signals could be used to train individuals to recognize certain stimuli as indicating a superior opponent. Pitting trained animals against unfamiliar contestants with variations on the signal could demonstrate whether (i) individuals can learn to recognize an opponent's competitive ability based on a novel stimulus, (ii) individuals categorize opponents based on signal characteristics, and (iii) if there are peak shift phenomena in which especially strong responses are obtained to stimuli that go beyond the previously experienced range of signal variation, indicating a potential mechanism for the evolution of aggressive signal exaggeration [82].

Box 3 – Controversies over assessment strategies and the role of cognition

That animals rarely use physical attacks to resolve contests posed a theoretical puzzle that was solved with game theory models examining when more 'peaceful' assessment strategies could be evolutionarily stable [83]. Many of these models involve contestants differing in RHP, with the behaviors expressed during contests allowing for the assessment of contestant RHP, settling contests in favor of the superior individual [11]. Most models investigate one of three broad categories of assessment strategy: (i) mutual assessment, (ii) self-assessment, or (iii) cumulative assessment [33].

458

459 The mutual assessment strategy was frequently tested by empiricists because it makes the
460 simple prediction that contests between evenly-matched opponents should be longer and
461 more escalated than contests between individuals with large RHP differences [80]. However,
462 this prediction was later demonstrated to also apply to other assessment strategies, and
463 experimental designs that discriminate between mutual- and self-assessment strategies have
464 only recently been developed [33,84]. Many recent studies give evidence for self- rather than
465 mutual-assessment [85,86], leading to some backlash against the idea that mutual assessment
466 is the prevalent means by which animals resolve contests. Cognition is invoked in these
467 arguments: mutual assessment is claimed to be more 'cognitively complex' because it
468 requires evaluation and relative comparison of both competitors' traits whereas self-
469 assessment only requires input from an individual's own state [7]. However, there is
470 disagreement about whether mutual-assessment models require cognitively advanced
471 comparisons, or whether performing such comparisons is even cognitively challenging
472 [87,88].

473

474 Without a cognitive perspective on animal contests, this controversy will remain unresolved
475 because little is known about the cognitive mechanisms of assessment. Cognition is treated as
476 a black box both in models of assessment strategies and in arguments that strategies differ in
477 their cognitive requirements. Does mutual assessment truly involve relative comparison
478 requiring extensive memory and categorization abilities, or is it a simple modification of self-
479 assessment with additional sensory input from opponents? Considering cognitive
480 mechanisms also alters the predicted relationships between contestant RHP and contest
481 duration under different assessment strategies. In particular, it has been argued that, for a
482 given RHP difference between contestants, under mutual assessment contest duration should

not vary with absolute competitor RHP [33]. However, relative assessments become more difficult at larger absolute stimulus values [89]; thus under mutual assessment and a constant RHP difference, contest duration should be an increasing function of absolute competitor RHP. Therefore, positive relationships between individual RHP and contest duration are not always diagnostic of self-assessment.

Box 4 – Cognition and contest theory

Animal contests have received much attention from theoretical biologists [32]. However, cognition is rarely considered in models of strategic contest behavior. A major gap in theory could be addressed by examining the conditions under which learning or other cognitive mechanisms can evolve as a component of evolutionarily stable contest strategies. Below we briefly describe some of the few theoretical models examining the role of cognition in animal contests.

Stamps and Krishnan [90] developed a model of territory settlement with a key role for learning. As individuals move through space they can encounter other individuals and engage in aggressive interactions. These contests form the basis for associative learning, with individuals reducing their probability of returning to an area after associating it with the negative effects of encountering aggressive competitors. The model reproduced several spatial patterns known from nature including the formation of exclusive territories when levels of aggression are high. This model could be extended to explore how patterns of space use and cognitive variation explain individual variation in the susceptibility to density-

dependent effects, ultimately affecting distribution patterns across heterogeneous landscapes, and explaining when and why deviations from the ideal free distribution are observed.

Mesterton-Gibbons and Heap [9] developed an extension of the hawk-dove game to explore factors that lead contestants to adopt either self- or mutual-assessment strategies. An important component of the model is the incorporation of trade-offs between obtaining information on opponents and the resultant costs of revealing information to opponents. Although not explicitly cognitive, this model could easily be expanded to incorporate cognitive processes and fits with the framework proposed here, because it examines the factors underlying variation in the expression of strategic contest behavior based on the costs and benefits of information gathering.

Lee and colleagues [50] developed a model based on the producer-scrounger game to examine the conditions under which individuals use social information when foraging instead of searching for resources on their own. An individual's competitive ability relative to the distribution of competitive abilities in the population was a key parameter in determining the profitability of producer versus scrounger (social information use) tactics. However, the benefits of scrounging for individuals of high competitive ability depended on resource availability. Thus, this model demonstrates links between information gathering, contest outcome and ecology, as proposed by our framework (Figure 1).

Outstanding questions box

-*What is the role of perception in mediating cognitive processes underlying contest behavior?*

-*How do multiple cognitive abilities interact with one another, and with non-cognitive mechanisms to determine contest behavior?*

-*What is the role of ecology, social structure, and constraints in explaining between-species variation in the importance of cognition in contests?*

-*What is the quantitative genetic basis of cognitive performance in contests, in terms of the components of variation underlying individual traits, and the extent to which different kinds of traits are genetically correlated with one another and fitness?*

-*Are cognitive abilities used in contests predictive of cognitive abilities in other contexts? Does selection result in adaptive cognitive specializations for contests, or for more general cognitive performance across contexts?*

- *How well do animals understand the intentions and relations of others while observing contests? Can contests give any insights into the debates surrounding the existence of a theory of mind in animals?*

Glossary

Assessment strategy: The function relating information gathered before and during the contest to the expression of contest behaviors, especially decisions of whether to persist, withdraw or escalate.

Categorization: The processes by which stimuli are assigned to distinct groups that are distinguished from other such groups of stimuli.

Classical conditioning: Learning to associate one cue with a second such that a response initially given only to the second cue can eventually be elicited by the first cue alone.

Cognition: The processes involved in the acquisition, processing, retention and use of information from the environment [18].

Cognitive ability: A cognitive mechanism involved in the performance of a particular behavior; individuals vary in the effectiveness of these mechanisms, and hence in cognitive ability.

Cognitive performance: The realized outcome of a task requiring cognition, which is determined by both cognitive ability and environmental factors including motivation, motor performance and ecological context.

Contest: A direct and discrete behavioral interaction determining ownership of an indivisible resource unit [2].

578

579 **Cumulative assessment**: An assessment strategy in which an individual's contest behavior is
580 determined by its own characteristics and no opponent assessment takes place, but in which
581 opponents can nonetheless exert an influence on individual persistence by inflicting direct
582 costs [91].

583

584 **Dear enemy effect**: The phenomenon in which territory owners respond less aggressively to
585 familiar neighbors than to strangers [42].

586

587 **Habituation learning**: A decrement in response to a repeated stimulus not due to sensory
588 adaptation or motor fatigue.

589

590 **Learning**: A change in cognitive state as a result of experience that can influence future
591 behavior [18].

592

593 **Mutual assessment**: An assessment strategy in which an individual's contest behavior is
594 determined by gathering information on an opponent's RHP relative to its own RHP [33].

595

596 **Operant conditioning**: Learning to associate a behavior with its consequences.

597

598 **Resource-holding potential**: An individual's absolute fighting ability [11].

599

600 **Self assessment**: An assessment strategy in which an individual's contest behavior is
601 determined only by its own characteristics [33].

602

603 **Social eavesdropping**: Occurs when an animal obtains information from interactions
604 between conspecifics by observing, rather than directly participating in the interaction.
605
606 **Theory of mind**: An understanding of the intentions and beliefs of others.
607
608 **Transitive inference**: Inferring unknown relationships from known relationships. In the
609 context of animal contests, animals might observe contests and infer that if individual A
610 defeats individual B, and individual B defeats individual C, then individual A should defeat
611 individual C.
612
613 **True individual recognition**: The ability to recognize an individual from its distinctive
614 characteristics and associate those characteristics with other information about that
615 individual, as opposed to recognizing different classes of individuals [21].
616
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619

620 Table 1. Selected studies providing evidence for a role of cognition in contest behavior, along with potential socioecological consequences,
621 divided into behaviors occurring at different time points relative to a contest.
622

Cognitive mechanism(s)	**Contest behavior**	**Species**	**Description**	**Possible socioecological consequence**	**Refs**
(I) Before contests					
Imitation learning, operant conditioning	Aggressive signal development	*Melospiza melodia*	Songs used in territory defense are learned from neighbors' interactions.	Contest strategies influence cultural signal evolution.	[92]
Classical conditioning	Rival anticipation	*Trichogaster trichopterus*	Classical conditioning allows anticipation of intruder approach.	Selection for territoriality & development of alternative "sneaker" tactics.	[29]
Recognition learning and memory	Pre-fight assessment	*Poecile atricapillus*	Relative threat of intruders assessed by integrating information from eavesdropping on multiple song contests.	Selection for private communication and/or victory displays.	[93]

Transitive inference	Pre-fight assessment	*Julidochromis transcriptus*	Rival dominance inferred by both direct previous experience and indirect experience from contests with common opponents (in unfamiliar rivals).	Cognitive mechanisms influence speed of formation and stability of dominance hierarchies.	[44]
Categorization	Pre-fight assessment	*Macaca mulatta*	Dominance can be learned as a categorical concept from video playbacks of aggressive individuals.	Evolution of social cognition.	[94]
(ii) During contests					
Perception	Rival assessment (dyadic contests)	*Teleogryllus oceanicus*	Contests more escalated when males prevented from exchanging acoustic signals.	Selection for specialized aggressive communication system.	[95]
Perception	Contest resolution	*Neogobius melanostomus*	Contests in contaminated water less likely to have clear winner and loser.	Anthropogenic disturbance influences costs and benefits of aggressive behavior.	[96]

Comparative judgement	Resource-value assessment	*Clibanarius vittatus*	Attackers in fights over shells in hermit crabs assess both own gain and likely gain of defender by swapping shells	Resource availability affects likelihood and severity of contests.	[97]
Numerosity	Rival assessment (group contests)	*Panthera Leo*	Individuals assess numerical asymmetry in group size during intergroup contests.	Evolution of higher-order cognitive traits, selection for social coordination.	[98]
(iii) After contests					
Recognition learning and memory	Winner/Loser effect	*Anolis carolinensis*	Loser effect only exhibited when individual faced with familiar rival.	Cognitive mechanisms influence speed of formation and stability of dominance hierarchies.	[76]
Recognition learning and memory	Dear enemy effect	*Ctenomys talarum*	Individuals recognize odors of familiar previous rivals and respond less aggressively towards them.	Stabilization of territorial resource defense strategies.	[99]
Recognition learning and memory	Dear enemy effect	*Vireo olivaceus*	Less aggression directed towards neighbors despite potential difficulties in recognition from large song repertoire size.	Cognitive abilities relax constraints on selection on song variation, which might play role in other contexts (e.g., mate selection).	[100]

623

624 [a]Perception should play a role in the expression of all aggressive behaviors and cognitive mechanisms. It is not listed explicitly in each entry

625 unless it is the focal mechanism of the study.

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